

# Predation by *Nucella cingulata* (Linnaeus, 1771) on Mussels, Particularly *Aulacomya ater* (Molina, 1782)

by

PATTI A. WICKENS AND CHARLES L. GRIFFITHS

Zoology Department, University of Cape Town, Rondebosch 7700, South Africa

*Abstract.* The whelk *Nucella cingulata* (Linnaeus, 1771) is abundant in the rocky intertidal zone of Marcus Island, South Africa, where it feeds on the mussels *Aulacomya ater* (Molina, 1782), *Choromytilus meridionalis* (Krauss, 1848), and *Perna perna* (Linnaeus, 1758). *Aulacomya ater* appears to be the preferred prey. The distribution of boreholes drilled in mussel shells collected from the field appears to be random, but borehole diameter is an increasing function of prey shell length. Laboratory feeding experiments confirm that larger individuals of *N. cingulata* drill wider boreholes and preferentially select bigger mussels. The energy value of food consumed increases rapidly with predator size, but this is accomplished by taking progressively larger prey rather than more of them. The overall impact of *N. cingulata* on the *A. ater* population is estimated and compared with that of other invertebrate predators. Although many small mussels are taken by predators, this often acts merely to reduce the intense intraspecific competition for space to which juvenile mussels are frequently subjected.

## INTRODUCTION

*Nucella cingulata* (Linnaeus, 1771) is a predatory whelk that lives in the intertidal and subtidal zones of rocky shores along the west coast of southern Africa. Its principal prey items are the three species of mussel that occur in the area, namely the ribbed mussel *Aulacomya ater* (Molina, 1782), the black mussel *Choromytilus meridionalis* (Krauss, 1848), and the brown mussel *Perna perna* (Linnaeus, 1758). *Nucella cingulata* attacks its prey by drilling a hole through the shell, using alternating mechanical and chemical processes, *i.e.*, rasping with the proboscis and secretion of acid by an accessory boring organ respectively, as described in related species by FRETTER & GRAHAM (1962). The flesh is subsequently extracted through the hole using the proboscis and consumed.

Predators utilizing this technique spend most of their time manipulating and ingesting prey and little in search and capture. BAYNE & SCULLARD (1978), for example, found that *Nucella lapillus* spent between 63 and 97 hours drilling and ingesting each prey item, and CONNELL (1970) discovered that *Thais* spp. spent approximately 70-80% of their feeding time in the process of drilling alone. Larger mussels naturally yield a greater amount of flesh and therefore more energy to the predator, but they also have thicker shells and therefore require a greater investment of time and energy in the boring process. Consequently,

one might expect each predator to select an optimum size of mussel, one that provides a balance between energy gained from the prey flesh and effort put into obtaining it. Many boring predators do indeed tend to select particular species and sizes of prey, and many position their boreholes in certain areas of the shell in order to minimize the time spent manipulating prey and to maximize the energy returned per unit effort expended. Such parameters have been studied in a variety of boring gastropods from different parts of the world. Feeding rates of *Polinices duplicatus* Say (EDWARDS & HUEBNER, 1977), *Nucella lapillus* Linnaeus (BAYNE & SCULLARD, 1978), and *Natica tecta* Anton (GRIFFITHS, 1981b) have been calculated, while observations on drilling behavior, borehole location, and feeding strategies have been made for *Lunatia alderi* (Forbes) (Verlaine, 1936 quoted by FRETTER & GRAHAM, 1962, and ANSELL, 1960), *Nucella lapillus* (MORGAN, 1972; HUGHES & DUNKIN, 1984), *Natica catena* (da Costa) (NEGUS, 1975), *Thais lamellosa* Gmelin (CAREFOOT, 1977), *Dicathais aegrota* Reeve (BLACK, 1978), and *Natica tecta* (GRIFFITHS, 1981b) among others.

The principal objective of this study is to determine whether *Nucella cingulata* preferentially select prey by species or shell length, and if so, to record the prey preference and consumption rates of predators of various sizes. Observations are also made of the location of boreholes

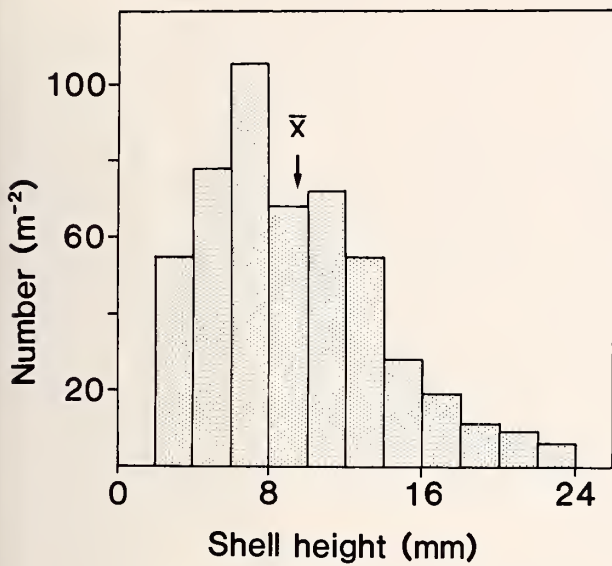


Figure 1

Size-frequency distribution of *Nucella cingulata* on Marcus Island ( $n = 336$ ). Mean density =  $492 \pm 759$  individuals per meter squared.

and relationships between predator and prey size and borehole diameter. The overall energy requirements of the predator population are calculated and compared with the size of the prey resource on Marcus Island. From this, the effect of *N. cingulata* on the mussel population can be determined and the energy requirements of *N. cingulata* compared with those of other mussel predators that occur on the same coast, namely the rock lobster *Jasus lalandii* (Milne Edwards) (GRIFFITHS & SEIDERER, 1980), the boring gastropod *Natica tecta* (GRIFFITHS, 1981b), the starfish *Marthasterias glacialis* (Linnaeus) (PENNEY & GRIFFITHS, 1984), and the African Black Oystercatcher, *Haematopus moquini* Bonaparte (HOCKEY, 1984). Finally, an attempt is made to rate the importance of predation to other population regulating mechanisms.

## METHODS AND RESULTS

### FIELD STUDIES

A field survey was conducted during April 1983 when a total of thirteen quadrat samples was collected from various tidal levels at each of six study sites on Marcus Island, Saldanha Bay, South Africa ( $33^{\circ}02'S$ ,  $17^{\circ}58'E$ ). The information obtained from each sample included quadrat area, numbers and size distributions of each of the mussel species (*Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna*), and of the whelk (*Nucella cingulata*), as well as shell length, borehole diameter, and borehole position for drilled shells of each mussel species remaining in the beds. Data from the thirteen quadrat samples have been combined here to give a general pattern for Marcus Island. All correlations have been determined using Pear-

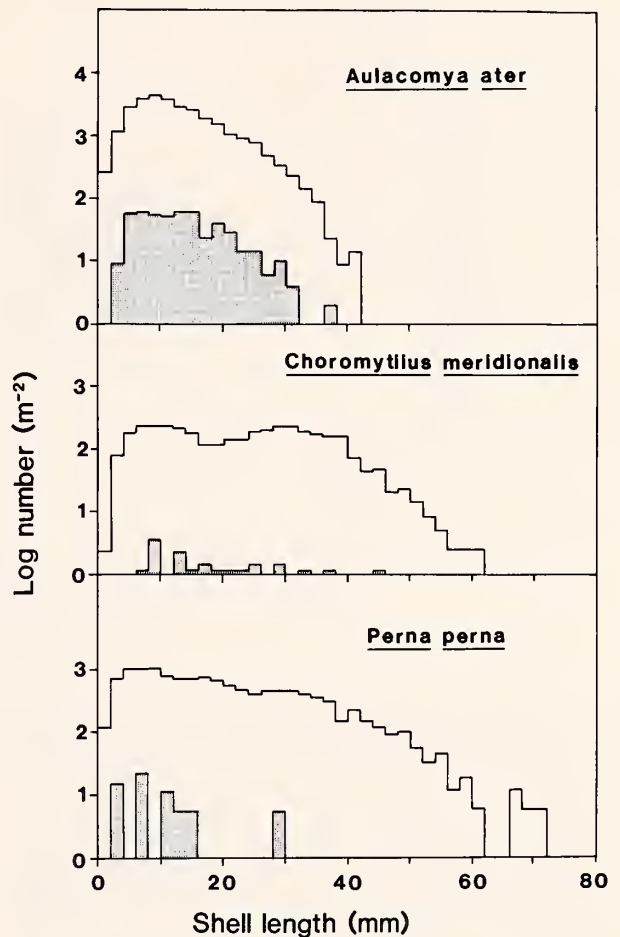


Figure 2

Size-frequency distributions of live and drilled (shaded area) *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* on Marcus Island.

son's product moment correlation coefficient. Mussel size is taken as the distance from the umbo to the opposite tip of the valves. The size of *N. cingulata* is taken as the distance from the base of the shell to the top of the last whorl.

### Sizes and Abundances of Predator and Prey and Quantification of Mussel Predation

A size-frequency distribution for *Nucella cingulata* from Marcus Island is shown in Figure 1. The population density was extremely high and extremely variable at  $492 \pm 759$   $m^{-2}$ . Individual size was small, with a mean shell height of 9.5 mm. Size-frequency distributions of both living and drilled *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* are given in Figure 2. Only mussel species are considered here because a negligible number of other drilled invertebrate prey, such as the slipper limpet *Crepidula porcellana* Lamarck, were found. Table 1

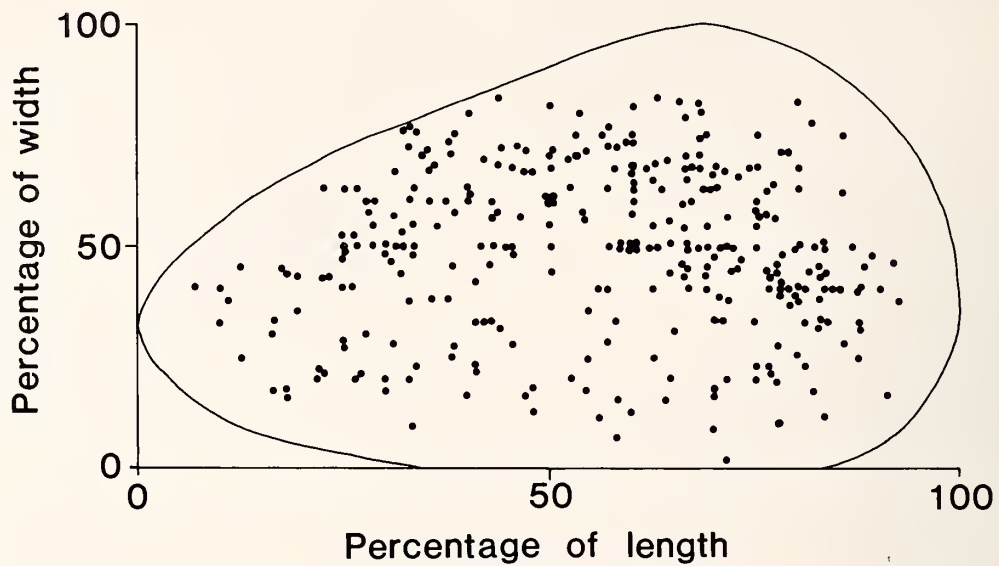


Figure 3

Position of 316 boreholes on *Aulacomya ater* shells collected from Marcus Island.

summarizes the statistics of both living and drilled individuals of the three mussel species. The population size-frequency distributions for *N. cingulata* and all three mussel species are skewed to the right, with the result that the mean size is higher than the population mode. *Aulacomya ater* is the most abundant of the mussel species (64.1%) and appears to be the preferred prey of *N. cingulata* (89.2% of all prey). For all three mussel populations combined, the mean prey size (16.2 mm) is approximately the same as the mean population size (15.5 mm), but drilled *P. perna* were significantly smaller than the population average. *Nucella cingulata* takes similar size ranges of each prey species, although the mean size of *C. meridionalis* taken is slightly greater than that of the other two species.

#### Location of Boreholes in Shells Collected in the Field

The number of drilled shells of each species and the number of boreholes per drilled shell are given in Table 2. From the total of 323 drilled mussels recovered, there were 24 mussels (7.4%) that had more than one borehole completely penetrating the shell. No *Choromytilus meridionalis* had more than one borehole, but 7.6% of all drilled *Aulacomya ater* and 16.7% of *Perna perna* had been drilled more than once. The position of the borehole on each drilled shell for each of the three species was plotted as the percentage of the shell length against the percentage of the shell width. For *C. meridionalis* and *P. perna*, there were too few borehole data ( $n = 23$  and  $n = 14$  respec-

Table 1

Population statistics for living and drilled *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* on Marcus Island.

Species	Living populations				Drilled shells				Drilled shells as percentages of their populations
	Density (m <sup>-2</sup> )	Percentage of all mussels	Mean length (mm)	Size range (mm)	Density (m <sup>-2</sup> )	Percentage of all mussels	Mean length (mm)	Size range (mm)	
<i>Aulacomya ater</i>	28,528 ± 33,086	64.1	13.0 ± 6.6	1-42	487	89.2	15.7 ± 6.6	3-40	1.74
<i>Choromytilus meridionalis</i>	3593 ± 1823	8.1	22.7 ± 12.0	1-62	16	7.1	21.8 ± 10.2	7-46	0.46
<i>Perna perna</i>	12,356 ± 9738	27.8	19.3 ± 12.6	1-72	62	3.7	12.3 ± 7.1	3-32	0.30
Total	44,477	100.0	15.5	1-72	566	100.0	16.2	3-46	1.27

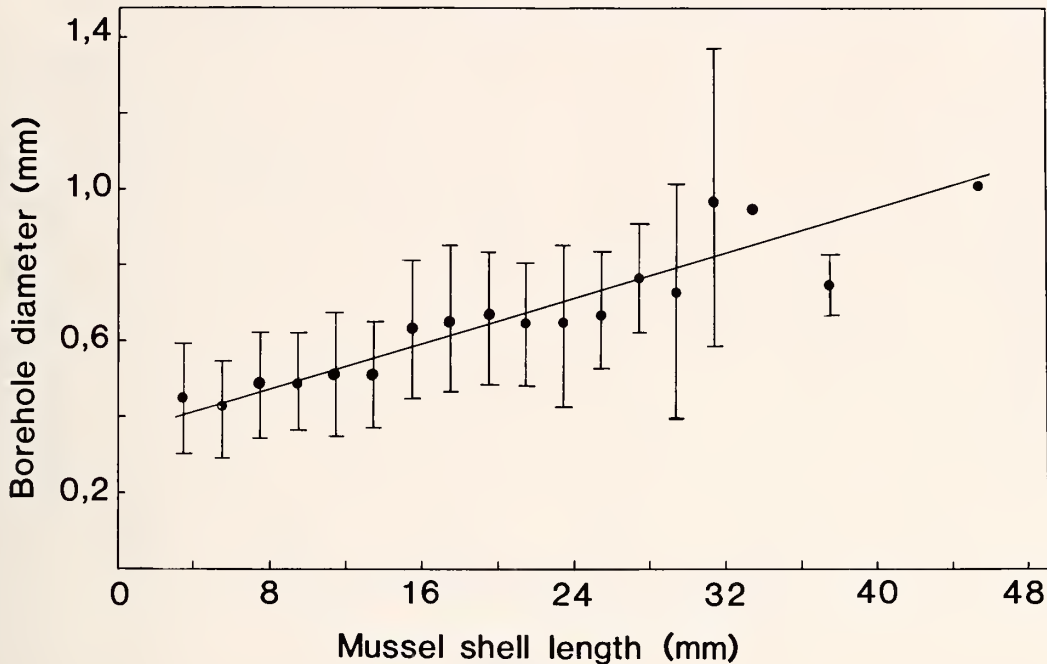


Figure 4

Borehole diameter as a function of mussel shell length for 353 boreholes drilled into all three mussel species collected from Marcus Island. For convenience, a mean value of each 2-mm size class is represented with vertical bars showing one standard deviation either side of this mean.

tively) to show an aggregation in any particular region. Figure 3 shows the borehole positions for *A. ater*. Although the margins of the shell valve are avoided, there does not appear to be a concentration of boreholes in any particular locality. Of the drilled shells of all three species, 48.6% were drilled on the left valve while 51.4% were drilled on the right valve. A chi-square test showed that this difference was not significant ( $n = 353, 0.05 < P < 0.01$ ).

**Borehole Diameter versus Mussel Size**

In order to ascertain whether larger mussels had been preyed upon by larger *Nucella cingulata*, borehole diameter was measured and related to the shell length of each drilled mussel. Both outside and inside borehole diameters were measured, but the outside measurement was ultimately used as the standard index of size. Boreholes were measured using a dissecting microscope fitted with a net-scale graduated to 0.1 mm and a mean value calculated for mussels of each 2-mm size class from 3–4 mm to 45–46 mm. Figure 4 shows a plot of mean outside borehole diameter for each 2-mm size class against mussel length. The inside borehole diameter varies less with increasing mussel size, having a slope with half the gradient of that for outside diameter. The correlation between borehole diameter and mussel size is significant ( $n = 323, 0.025 < P < 0.005$ ), and a regression line fitted to the data gives

the relationship: borehole diameter (mm) =  $0.323 + 0.015 \times$  mussel length (mm) ( $r = 0.918$ ).

**LABORATORY STUDIES**

Because *Aulacomya ater* appeared to be the most abundant prey species taken by *Nucella cingulata*, only this species was considered in our experimental studies. Specimens of *N. cingulata* and *A. ater* were collected from Marcus Island and taken to the laboratory, where prey size-selection and predation-rate experiments were conducted. The an-

Table 2

Number of boreholes found in shells of *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* collected from Marcus Island.

Species	Number of holes in shell					Total number of boreholes	Total number of drilled shells
	1	2	3	4	5		
<i>Aulacomya ater</i>	266	18	3	0	1	316	288
<i>Choromytilus meridionalis</i>	23	0	0	0	0	23	23
<i>Perna perna</i>	10	2	0	0	0	14	12
Total	299	20	3	0	1	353	323

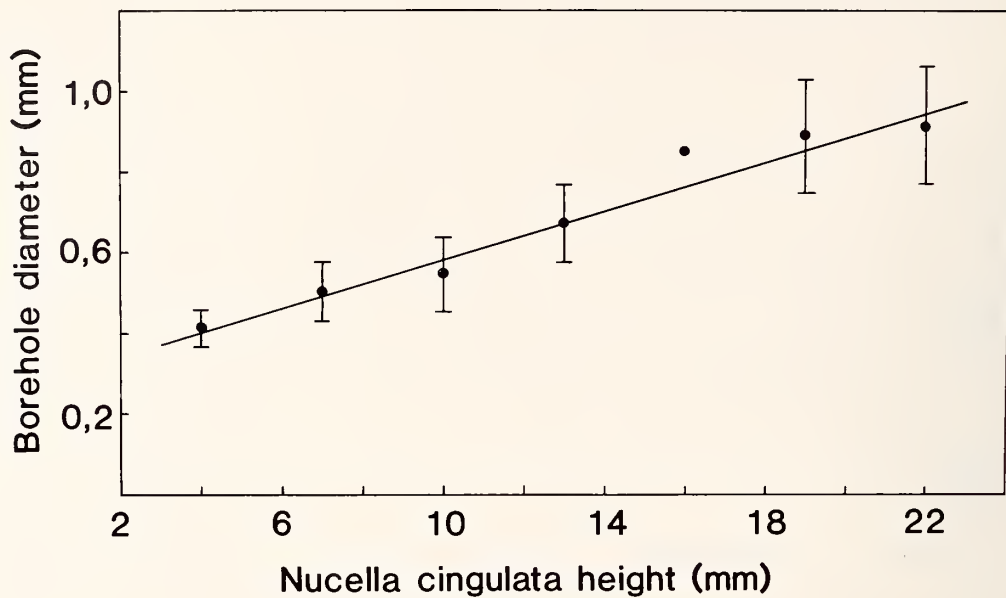


Figure 5

Borehole diameter as a function of *Nucella cingulata* height for 78 boreholes drilled into *Aulacomya ater* shells in the laboratory. For convenience, a mean value for each 2-mm size class is represented here with vertical bars showing one standard deviation on either side of this mean.

imals were maintained in large aquaria connected to a flow-through seawater system at a constant temperature of 14.5°C (which is approximately the temperature of the seawater at Marcus Island). An acclimation period of 15 days was allowed during which time the specimens of *N. cingulata* were supplied with excess *A. ater* of a wide size range. The whelks ( $n = 33$ ) were then separated into seven 3-mm size classes (3–5 mm to 21–23 mm), each group being placed in a separate plastic floating ring with a net base and floated in a large tank. In two of the size classes of *N. cingulata* only a few individuals were available, so not all of the rings were initially supplied with the same number of individuals. The specimens of *A. ater* were also separated into eight 5-mm size classes (1–5 mm to 36–40 mm) and each of the seven rings supplied with six individuals from each size class of mussel.

The tanks were subsequently examined every 4 days for a total period of 32 days. At each sampling all the drilled mussels were removed and measured and replaced with other individuals from the same size class. Any dead individuals of *N. cingulata* were also removed and, where possible, replaced with other individuals from the same size class. Additional specimens of *N. cingulata* were kept in a separate tank and were fed *Aulacomya ater* to sustain them, so that they would not be starved if needed in the experiments. Because the number of predators per size class during each 4-day sampling period was not constant, the consumption rate per *N. cingulata* was calculated independently over each 4-day period and subsequently averaged.

#### Location of Boreholes in Shells Collected in the Laboratory

No shell with more than one complete borehole was found during the laboratory experiments. The positions of the boreholes were similar to those in shells recovered from the field. Of the drilled shells, 42.3% were drilled on the left valve and 57.7% on the right valve. A chi-square test showed that this difference was not significant ( $n = 78$ ,  $0.05 < P < 0.01$ ).

#### Borehole Diameter versus *Nucella cingulata* Size

The mean outside and inside borehole diameters were calculated for *Aulacomya ater* shells drilled by *Nucella cingulata* of each of the size classes. The slope for inside diameter against *N. cingulata* size was again half that for outside diameter. A plot of mean outside borehole diameter against *N. cingulata* size is given in Figure 5. The correlation between borehole diameter and *N. cingulata* size is significant ( $n = 78$ ,  $0.025 < P < 0.005$ ), and a regression line fitted to the data produced the relationship: borehole diameter (mm) =  $0.281 + 0.03 \times N. cingulata$  height (mm) ( $r = 0.980$ ).

#### Drilled *Aulacomya ater* Size versus *Nucella cingulata* Size

The mean size of *Aulacomya ater* drilled by *Nucella cingulata* of each 3-mm size class is shown in Figure 6. The correlation between *N. cingulata* size and shell length

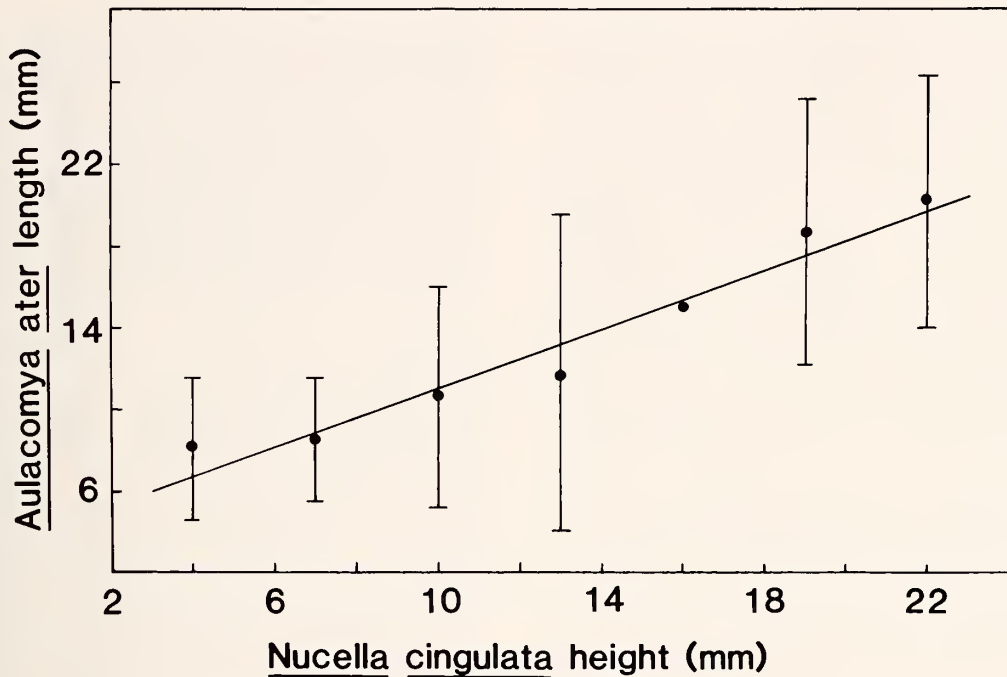


Figure 6

Length of 78 *Aulacomya ater* consumed in a laboratory experiment as a function of *Nucella cingulata* height. For convenience, a mean value for each 2-mm size class is represented here with vertical bars showing one standard deviation on either side of this mean.

of prey taken is significant ( $n = 78, 0.025 < P < 0.005$ ), and a regression line fitted to the data produced the relationship: *A. ater* length (mm) =  $3.632 + 0.734 \times N. cingulata height (mm) ( $r = 0.978$ ).$

**Predation Rate**

**Number of prey consumed:** For each *Nucella cingulata* size class, the number of *Aulacomya ater* consumed per individual per day was calculated (Table 3). The mean consumption rate was  $0.08 \pm 0.035$ , but there was no apparent relationship between the number of prey consumed per day and predator size.

**Energy consumption:** The dry flesh weights of different sized specimens of *Aulacomya ater* (5–25 mm) were measured, and the energy value of the flesh was determined by bomb calorimetry. The relationship between *A. ater* dry weight and size is significant ( $n = 90, 0.025 < P < 0.005$ ), the relationships being: (1) *A. ater* dry weight (mg) =  $0.025 \times A. ater$  length (mm)<sup>2.358</sup> ( $r = 0.889$ ) and (2) *A. ater* energy value =  $18.27 \pm 0.95$  kJ/g dry weight.

Because no flesh appeared to remain behind in the discarded mussel shells, it was assumed that *Nucella cingulata* ingests its prey with 100% efficiency. Contrary results have been found in, for example, *Polinices duplicatus*, which consumes only the visceral portion of the clam *Mya arenaria* Linnaeus (EDWARDS & HUEBNER, 1977), and we

recognize that there is likely to be loss of some semiliquid material (*e.g.*, DAGG, 1974); however, we were unable to quantify this. Thus, for each size class of *N. cingulata*, all the *Aulacomya ater* drilled in each of the eight 4-day sampling periods were converted to energy equivalents, and the total amount of energy consumed per predator in each 4-day period was calculated. These values were then summed to give the total energy consumed per *N. cingulata* over the 32 days and converted to weekly energy values. A plot of energy consumed per *N. cingulata* per week

Table 3

Number of *Aulacomya ater* consumed per *Nucella cingulata* individual per day in laboratory experiments.

<i>Nucella cingulata</i> size class (mm)	Number of <i>Aulacomya ater</i> consumed per individual per day
3–5	0.07
6–8	0.12
9–11	0.11
12–14	0.10
15–17	0.02
18–20	0.07
21–23	0.05
Mean $\pm$ 1 SD	$0.08 \pm 0.035$

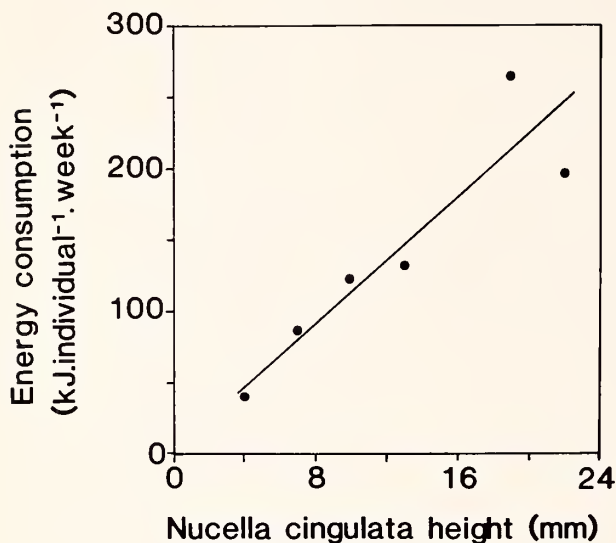


Figure 7

Average weekly energy consumption of *Nucella cingulata* during the laboratory experiments as a function of shell height.

against *N. cingulata* height is shown in Figure 7. One *N. cingulata* size class yielded only two data points and this group was excluded from the analysis. The correlation between mean energy consumption per week and *N. cin-*

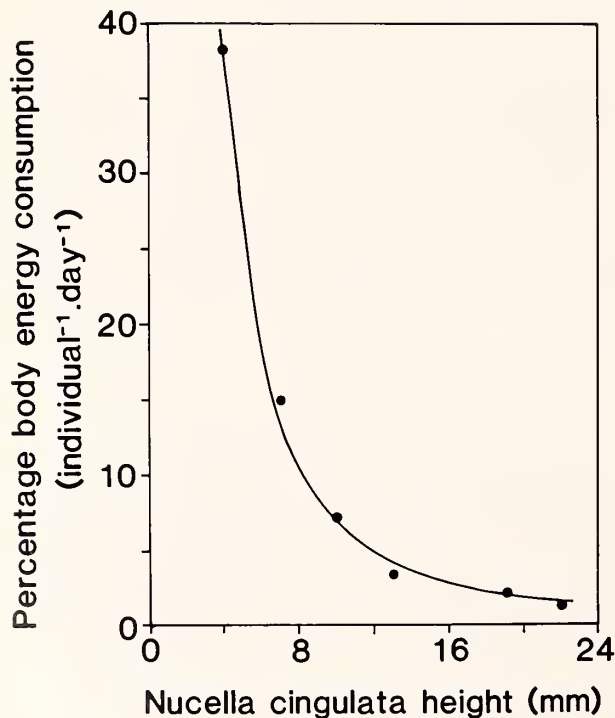


Figure 8

Percentage body energy consumption per *Nucella cingulata* individual per day as a function of shell height.

*gulata* size is significant ( $n = 6$ ,  $0.025 < P < 0.005$ ), and regression of the data produced a power curve with the relationship: energy consumption (kJ/week) =  $1.187 \times 10^{-2} \times N. cingulata$  height (mm)<sup>0.98</sup> ( $r = 0.967$ ).

**Percentage body energy consumed by *Nucella cingulata*:** The dry weights of different sized specimens of *Nucella cingulata* (6–25 mm) were measured, and the energy value of the flesh was determined by bomb calorimetry. The correlation between *N. cingulata* dry weight and size is significant ( $n = 29$ ,  $0.025 < P < 0.005$ ), the relationships being: (1) *N. cingulata* dry weight (mg) =  $0.012 \times N. cingulata$  height (mm)<sup>2.999</sup> ( $r = 0.984$ ), and (2) *N. cingulata* energy value =  $20.52 \pm 0.04$  kJ/g dry weight.

From these equations, the energy values of *N. cingulata* of different sizes were calculated. Using the daily consumption rates in conjunction with the energy values of *N. cingulata*, the percentage body energy consumed per day for different sized specimens of *N. cingulata* was obtained. A plot of percentage body energy consumed per day by different sized *N. cingulata* is given in Figure 8. The correlation between percentage body energy consumed and *N. cingulata* size is significant ( $n = 6$ ,  $0.025 < P < 0.005$ ), and fits a power curve with the relationship: percentage body energy consumed per individual per day =  $5.263 \times 10^2 \times N. cingulata$  height (mm)<sup>-1.912</sup> ( $r = -0.996$ ).

## DISCUSSION

### Prey Selection

Our field surveys showed that *Nucella cingulata* preys upon all three of the mussel species present on Marcus Island. *Aulacomya ater* appears to be the preferred prey because it comprises 64% of the living mussel community, but makes up 89% of the natural diet of *N. cingulata* (as indicated by numbers of drilled shells found in the field). There are several possible reasons for this preference for *A. ater*. It may be selected simply because it is the most abundant and hence most easily located prey species. The tidal level at which *N. cingulata* is most abundant is that at which *A. ater* is most dense. This may be because of similar tolerance of the two species to exposure, rather than simply an aggregation of predators in the region of maximum prey availability. One factor that certainly contributes to the greater vulnerability of *A. ater* is that the population consists almost entirely of small individuals (<40 mm) that fall within the size range available as prey to *N. cingulata* (3–46 mm). By contrast, many of the specimens of *Choromytilus meridionalis* and *Perna perna* exist in a "refuge in size" (PAINE, 1965) over 46 mm, where they are not available to the small individuals of *N. cingulata* that dominate the population in this area. There is no doubt, however, that there is a definite preference for *A. ater* even within the available size range as prey, as can be seen from Figure 2.

Laboratory experiments showed that the size of prey taken by individual *Nucella cingulata* is an increasing func-

tion of predator size (Figure 6), a finding that is confirmed by studies of other boring gastropods, such as *Nucella lapillus* (BAYNE & SCULLARD, 1978) and *Polinices duplicatus* (EDWARDS & HUEBNER, 1977). The size of predators can also be inferred from borehole diameter (Figure 5), so our laboratory results could be validated in the field by correlating borehole diameter with length of drilled mussels. Field surveys indeed confirmed that larger mussels had, on average, wider boreholes (Figure 4) and, hence, had been preyed upon by larger predators.

#### Location of Boreholes

Some boring gastropods selectively drill in a particular location of the prey shell. CAREFOOT (1977), for example, calculated that 98% of the boreholes drilled by *Thais lamellosa* on *Mytilus edulis* were found in the thinner regions of the prey shell, whereas HUGHES & DUNKIN (1984) found that *Nucella lapillus* reduced drilling time by approximately 27% by drilling through the thinnest areas of the shell. GRIFFITHS (1981b) found that the position of the boreholes drilled by *Natica tecta* on *Choromytilus meridionalis* were related to the way in which the predator holds its prey. MORGAN (1972) showed that the boreholes on *Cerastoderma edule* drilled by *Nucella lapillus* were determined by the way the cockle is held in the sand. *Thais lamellosa* (CAREFOOT, 1977), *Lunatia alderi* (Verlaine, 1936 quoted by FRETTER & GRAHAM, 1962), *Dicathais aegrota* (BLACK, 1978), and *Nucella lapillus* (HUGHES & DUNKIN, 1984) have been shown to drill boreholes over particular underlying organs. However, the boreholes drilled by *Nucella cingulata* appear to be randomly located over the entire central portion of the shell, with no preference for either valve. Several *Nucella lapillus* individuals have been observed to feed simultaneously on a single prey item (MORGAN, 1972; BAYNE & SCULLARD, 1978). Because 7.4% of all mussels drilled by *N. cingulata* on Marcus Island have more than one hole, it is possible that this may have resulted from a cluster of individuals feeding at the same time. Alternatively, some *N. cingulata* may, in error, drill into a mussel that has already been eaten, particularly if the mussel has not opened because of incomplete ingestion of the adductor muscle by the original attacker.

#### Predation Rate

The number of *Aulacomya ater* individuals consumed by *Nucella cingulata* shows no increase with predator size, the increased consumption rates of larger predators being attained by eating larger prey, rather than by taking more of them. Energy consumption is an approximately linear function of *N. cingulata* height (power value of 0.98). This is in contrast to the findings for *Natica tecta*, where energy consumption is approximately a cubic (power value of 2.9132) function of shell height (GRIFFITHS, 1981b). The two shells are, however, quite different in shape, *Natica tecta* having a more spherical shape and presumably in-

creasing in weight more rapidly with shell height. *Nucella cingulata* consumption, moreover, declines drastically from about 40.0 to 1.5% of body energy per day with increasing size, over the range of 3 to 23 mm (Figure 8). By comparison, BAYNE & SCULLARD (1978) showed that *Nucella lapillus* consumes between 15 and 1.5% of its body weight per day over a size range of 12 to 32 mm, while *Polinices duplicatus* consumes between 1.3 and 0.9% of its body weight per day over a size range of 19 to 45 mm (EDWARDS & HUEBNER, 1977). The lower limits of the percentage body energy/weight consumed for the larger animals of these different species are comparable, while the smaller specimens of *N. cingulata* take a greater percentage, as might be expected as a result of their higher weight-specific metabolic rate.

#### Exploitation of *Aulacomya ater* on Marcus Island

Using our laboratory relationship between energy consumption and size of *Nucella cingulata*, together with its size-frequency distribution and density on Marcus Island, the energy requirement of the entire population can be calculated as  $3475 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ . The standing crop of the entire *Aulacomya ater* population was  $7939 \text{ kJ}\cdot\text{m}^{-2}$ , while the energy available from individuals in size classes accessible to *N. cingulata* is  $7437 \text{ kJ}\cdot\text{m}^{-2}$  (94% of the total). It is of interest to compare this predation rate with those of other mussel predators that occur in the same area. *Aulacomya ater* comprises only 16% of the diet of the African Black Oystercatcher, *Haematopus moquini*, on Marcus Island and its total annual take of mussels is estimated to be a relatively moderate  $878 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  (HOCKEY, 1984, and unpublished data). Three invertebrate predators, the rock lobster *Jasus lalandii*, the starfish *Marthasterias glacialis*, and the gastropod *Natica tecta* have also been studied. In their areas of maximal abundance and when feeding on the mussel *Choromytilus meridionalis*, these were predicted to consume annual totals of  $5835 \text{ kJ}\cdot\text{m}^{-2}$ ,  $6028 \text{ kJ}\cdot\text{m}^{-2}$  and  $9010 \text{ kJ}\cdot\text{m}^{-2}$  respectively (PENNEY & GRIFFITHS, 1984). Populations of *C. meridionalis*, however, have a greater standing crop ( $19,125\text{--}21,675 \text{ kJ}\cdot\text{m}^{-2}$ ) than those of *A. ater*, so that the percentage of standing crop taken in each case is remarkably similar, at 46% for *N. cingulata* consuming *A. ater* and between 28 and 44% for the three predators of *C. meridionalis*.

Although we recognize that laboratory feeding experiments may substantially overestimate consumption rates, the predation pressure exerted by each of these predators is nevertheless considerable and, if there were no mussel replacement, they would rapidly obliterate their prey populations. In reality, however, each species has been studied in its area of maximum abundance and there is only partial overlap in the distributions of the various species. Therefore, where one predator is particularly abundant, the others are often rare or absent, and where two or more predators are present, they frequently both occur at reduced densities. Nonetheless, our results suggest that pre-



dation rates of 30–50% of prey standing stock per annum are commonplace and these would significantly affect the density and size composition of the mussel beds, particularly because the majority of prey are taken from a particular "window" of size classes available to the predators.

If we consider the overall impact of predation on settlements of mussels, however, we must remember that juvenile mussel populations have an extremely high production-to-biomass (P/B) ratio which allows them to support considerable predation pressure without any decline in standing crop. In *Aulacomya ater*, for example, the P/B ratio is 29.5 at 5 mm (all of which goes into growth), declining below 2.0 above 45 mm (most of which is expended in reproductive output) (GRIFFITHS & KING, 1979). Secondly, GRIFFITHS (1981a) has shown that juvenile *Choromytilus meridionalis* normally settle at densities of some tens of thousands of individuals per square meter, whereas the maximum packing density of adults over 50 mm is of the order of one thousand per square meter. These figures may not be directly applicable to *A. ater*, which can form multilayered beds, but a mortality of 90% or more is still to be expected over this growth period and will be accomplished by intraspecific competition for space should there be little or no mortality through predation.

Populations of juvenile mussels can thus absorb considerable losses to predation while remaining at maximum population density in terms of substrate carrying capacity. The actual rate of loss that can be tolerated while maintaining 100% cover will vary with the growth rate, but will probably be at least equal to the standing crop, because the P/B ratio of mussels of the size range available to predators is at least two. It is interesting to note that at the point where mussels grow into a "refuge in size," when they are no longer available to the majority of predators, they almost simultaneously arrive at a stable packing density at which they can continue to grow in length while fitting into the same area of substrate (see GRIFFITHS, 1981a, fig. 7).

In conclusion then, it appears that dense settlements of juvenile mussels can support large populations of predators during their logarithmic growth phase, while maintaining complete substrate coverage and constant or even increasing biomass and reproductive output (GRIFFITHS, 1981a). The slowing of growth rate that occurs as adult size is approached is accompanied by reductions both in the intensity of competition for space and in predation pressure, because the mussels reach a size at which they are relatively immune to predators. These adult populations persist until they become senile and die or are eliminated by some natural catastrophe, which may often take the form of a massive settlement of their own spat (GRIFFITHS, 1981a).

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